



Is Mixed-Species Living Cognitively Enriching? Enclosure Use and Welfare in Two Captive Groups of Tufted Capuchins (*Sapajus apella*) and Squirrel Monkeys (*Saimiri sciureus*)

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Abstract - Non-human primates have complex relationships with conspecifics and also other animals with whom they share their habitat in the wild. Some primates, such as capuchin monkeys (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*), naturally associate, with the potential to act as both proximate and ultimate influences on each other's behavior. There are a number of benefits to exhibiting such species in mixed communities in captivity, for instance the increased social complexity may provide environmental and social enrichment and appropriate cognitive challenges, ultimately enhancing their welfare in restricted captive enclosures. Monitoring how these species interact and utilize their available space is important for effective care and management. But despite this connection, there remains relatively little conclusive data on whether mixed groups of captive primates are cognitively enriching. This study examined patterns of space use in two mixed-species groups of *Sapajus* and *Saimiri* housed at the Living Links to Human Evolution Research Centre, RZSS Edinburgh Zoo. We predicted that if *Sapajus* and *Saimiri* were attracted to the presence of the other species then they would share the same space when in mixed enclosures. The data did not support this prediction. *Sapajus* showed a preference for central zones, while *Saimiri* spent more time in their exclusive indoor enclosure and appeared to prefer peripheral zones of their outdoor enclosures and close to doorways leading indoors. We conclude that while housing these species in a mixed exhibit may not be cognitively enriching it does provide appropriate cognitive challenges that can still enhance the welfare of individuals.

Keywords – Mixed-species zoo exhibit, Welfare, Social enrichment, *Sapajus*, *Saimiri*, Cognitive challenges

The captive environment presents numerous challenges in providing for the physical and psychological needs of its animal residents, and while efforts are commonly made to provide environmental enrichment, social enrichment is often neglected (Anderson, 1998; Visalberghi & Anderson, 1993). Wild animals face many day-to-day challenges requiring cognitive skills, whereas captive animals tend to live in more predictable and structured environments, in which their cognitive skills are infrequently challenged (Clark, 2011; Meehan & Mench, 2007). One way in which this can be achieved is to provide more cognitively challenging enrichment programs, though care should be taken to

ensure that the level of challenge is appropriate. For instance, captive animals should be able to actively control and explore their environment (Carlstead & Shepherdson, 2000), in addition to being able to either solve or escape problematic or stressful situations (Meehan & Mench, 2007). While stress is often associated as a sign of negative welfare, some would argue that the goal of animal husbandry is to provide conditions that enable animals to produce the full range of their behavioral repertoire, including stress and arousal (Chamove & Anderson, 1989; Moodie & Chamove, 1990).

The complexity of the social environment is claimed to have been a selective pressure for primate intelligence and has in turn been causally linked with encephalization (Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966). The Machiavellian Intelligence or Social Brain Hypothesis postulates that the evolution of intelligence is linked with social living and the potential problems and complexity that it poses (Byrne & Whiten, 1988; Dunbar & Shultz, 2007; Pasquaretta et al., 2014). While most social groups contain individuals of just one species, some species form polyspecific associations. The main reasons proposed for both single and mixed-species group living are foraging benefits and reduced predation risk (e.g., van Schaik, 1983). Most researchers acknowledge that a possible explanation regarding the formation of mixed-species groups is that it provides individuals with evolutionary benefits that may be unattainable in single-species groups (Heymann & Buchanan-Smith, 2000; Whitesides, 1989). For instance, mixed-species groups may be more likely to gain access to formerly unknown foraging sites and, by forming larger “mixed” groups, they can better detect predators (Huntingford, 1984; Stensland, Angerbjörn, & Berggren, 2003; Terborgh, 1983). Therefore, it is possible to infer that both conspecifics and congeners can drive the evolution of intelligence, and those individuals living in mixed-species groups may be more cognitively tested than in single-species groups, given close association with a different species with different behaviors (i.e., there is more to understand in order to function effectively).

Housing different species in a mixed exhibit is one way to provide captive animals with more challenging, complex social (and often physical) environments, and is now becoming commonplace in many zoos (Buchanan-Smith, Griciute, Daoudi, Leonardi, & Whiten, 2013; Hardie, 1997; Leonardi, Buchanan-Smith, Dufour, Macdonald, & Whiten, 2011; MacDonald & Whiten, 2011; Sodaro, 1999; Veasey & Hammer, 2010). The most successful combinations are those of naturally associating species (e.g., for New World primates; Buchanan-Smith, 2012), although some zoos exhibit sympatric species that do not associate (e.g., one species is arboreal and the other terrestrial; or one is diurnal, the other nocturnal). Occasionally individuals of different species are kept together for companionship or space reasons. Animals housed in mixed-species exhibits are likely to benefit from having larger enclosures than animals housed in single-species exhibits (Baker, 1992). Larger enclosures often facilitate increases in physical activity (e.g., more exploratory and play activities), social complexity and cognitive challenges, which can lead to improved welfare (Buchanan-Smith, 1999; Buchanan-Smith et al., 2013; Dalton & Buchanan-Smith, 2005; Heymann, Sicchar Valdez, & Tapia, 1996; Leonardi et al., 2010; Prescott & Buchanan-Smith, 2004; Thomas & Maruska, 1996). That being said, mixed-species exhibits have had varying degrees of success (see reviews by Buchanan-Smith, 2012; Sodaro, 1999). Therefore, it is important that groups are monitored carefully to ensure that interspecific aggression does not prove to be detrimental to the welfare of the animals (Buchanan-Smith, 2012; Buchanan-Smith et al., 2013; Dalton & Buchanan-Smith, 2005).

Despite these potential benefits, to our knowledge no studies have investigated whether mixed-species groups are cognitively enriching. Here we use Clark’s (2011) definition of cognitive enrichment, which is “...a task (or tasks) whose use (1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of well-being.” (p. 6, emphasis added). Although it would be difficult to provide conclusive evidence for cognitive enrichment (part 1) in mixed-species groups, Leonardi et al. (2010) compared behavior in single and mixed-species group conditions, and found that welfare indicators improved. This included a decrease in interspecific aggression (e.g., chase contact, displacement or threat display) and an increase in affiliative interactions (e.g., play, curious approach and moving together)

when the monkeys were in mixed-species groups compared to single-species groups, which provides supporting evidence for the second part of Clark's (2011) definition.

One can question whether individuals of the same (conspecific) and different (heterospecific) species may differ in the form of cognitive challenge they provide. The higher number of individuals in mixed-species groups compared to single-species groups may increase the challenge overall. In one sense the challenges presented by conspecifics and heterospecifics will be similar, with regard to competing for the same desired resources (such as food, water, or a preferred sleeping spot), or by providing social learning opportunities. However, the cognitive challenges related to conspecifics and heterospecifics may also differ particularly if from different genera as in our case, of *Sapajus* and *Saimiri*. For instance, individuals of the same species share many of the same physical and psychological characteristics, which may make them more predictable, whereas individuals of different species may be less predictable. With conspecifics, specific challenges are likely to relate to age and stage of development, for example mate competition in adults, or choice of play partner in juveniles. Indeed, white-faced capuchins (*Cebus capucinus*) are known to form coalitionary alliances (e.g., Perry, Barrett, & Manson, 2004) and selection of appropriate individuals will be key to their success. In contrast, the cognitive challenges posed by heterospecifics may be different due to factors such as contrasting size, physical abilities, and habitat preferences.

Ideally, to determine if enrichment is truly cognitive, satisfying part 1 of Clark's (2011) definition, an experimental approach should be used. However, other approaches may also be applied in order to determine the likelihood of whether animals are using their cognitive skills to solve problems and have control over their environment. In this paper we explore space use in two mixed-species groups of Guianan brown tufted capuchin (*Sapajus apella*) and Guianan squirrel (*Saimiri sciureus*) monkeys, housed at the Living Links to Evolution Research Centre in the Royal Zoological Society Scotland (RZSS) Edinburgh Zoo, in order to determine if the species are attracted to, or avoid each other and what this implies for their welfare. These two species are known to form temporary but stable polyspecific associations in the wild (Fleagle, Mittermeier, & Skopec, 1981; Klein & Klein, 1973; Podolsky, 1990; Terborgh, 1983). Of the Neotropical primate species known to associate, these two have the greatest relative difference in body size, with *S. apella* ($M_{\text{adult male}} = 3.0$ kg; $M_{\text{adult female}} = 2.4$ kg) being considerably larger than *S. sciureus* ($M_{\text{adult male}} = 0.74$ kg; $M_{\text{adult female}} = 0.64$ kg) (see Jack, 2007). Both species live in multi-male multi-female groups in the wild and include one alpha male (Boinski, 1999; Kinzey, 1997; Sussman, 2003). Though they are both omnivorous, *S. apella* are more frugivorous and *S. sciureus* more insectivorous, and due to this difference in diet and size these species tend to occupy different levels of the canopy (Fleagle et al., 1981; Terborgh, 1983). *Sapajus* tend to occupy the mid to lower levels of the main canopy, whereas *Saimiri* are more likely to be found in the understory (Boinski, 1999; Fleagle et al., 1981). It is therefore critical to take into consideration the niche partitioning of these two species, and to distribute resources so the animals do not compete over them, and to provide behavioral choice (Buchanan-Smith, 2012).

While there are clear benefits (in terms of the animals' biological and welfare requirements), to housing captive animals in larger and more naturalistic enclosures we should also consider how the animals utilize their captive environments, as even large enclosures can be of limited value, if the animals are unable to make use of all the space available (Estevez & Christman, 2006; Kerl & Rothe, 1996; Ogden, Finlay, & Maple, 1990; Paulk, Dieneske, & Ribbens, 1977; Ross & Lukas, 2006; Ross, Schapiro, Hau, & Lukas, 2009). For instance, Stoinski et al. (2000) found that a captive group of Western lowland gorillas (*Gorilla gorilla gorilla*) spent 50% of their time in less than 15% of their enclosures and displayed a preference for areas near structures, such as their holding building. Similarly, a study on lion-tailed macaques (*Macaca silenus*) found that they spent 43% of their time in less than half of their enclosure space (Mallapur, Waran, & Sinha, 2005). Additionally, having access to vertical space has been found to be important for arboreal non-human primates in captivity, as they tend to occupy higher areas (> 4 m) of their enclosures rather than being on the ground (Buchanan-Smith, Prescott, & Cross, 2004; Hebert & Bard, 2000; Leonardi et al., 2010; Poole, 1991; Ross, Calcutt, Schapiro, & Hau, 2011; Traylor-Holzer & Fritz, 1985). The age of individuals should also be considered. Juveniles, though smaller than

adults, are usually found to be more active than adults and therefore may have greater space requirements for physical development and play (Traylor-Holzer & Fritz, 1985; Wells & Turnquist, 2001).

The aims of this study were (a) to examine the differences in three-dimensional enclosure use (e.g., indoor/outdoor, height, location, and substrate) by two mixed-species groups of *Sapajus* and *Saimiri*; (b) to assess whether there is a difference in space use according to the age of individuals, for instance we might expect younger individuals to utilize more of the available space compared to adults; and (c) to assess whether the two species are attracted to each other, giving an indirect measure of the potential for cognitive enrichment. If both species are attracted by the presence of the other species then we expect them to share spaces. However, if the presence of the other species is threatening or stressful, we expect them to avoid certain areas and for the squirrel monkeys to remain in their exclusively accessed indoor enclosures. It must be noted that avoidance behavior is not necessarily indicative of poor welfare, and can be construed as an appropriate cognitive challenge for the animals.

Method

Subjects

Two mixed-species groups of Guianan brown capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*) housed at the 'Living Links to Human Evolution' Research Centre, within the RZSS Edinburgh Zoo were included in the study. There were 17 individuals of both *Sapajus* and *Saimiri* in the East exhibit, 18 individuals in the West *Sapajus* but only 9 in West *Saimiri* (see Table 1). Individuals were categorized as subadults at ≤ 4 years in *Sapajus* and ≤ 3 years in *Saimiri*, and individuals above these ages were categorized as adults. The *Sapajus* were distinctive enough to be identified individually, whereas identifying the *Saimiri* required artificial aids (chain collars with color coded beads), though these often fell off and so identification without these was also necessary.

Housing and husbandry. Both the West and East exhibits include an indoor enclosure for *Sapajus* (7 m x 4.5 m x 6 m high), an indoor enclosure for *Saimiri* (5.5m x 4.5m x 6m high), to which there is a size restriction on the entrance/exit, whereby only *Saimiri* can enter, and a shared outdoor enclosure of approximately 900m² (see Leonardi et al., 2010, for more details). Indoor temperatures were approximately 24°C, maintained using radiant ceiling heaters and the air conditioning system, and outdoor temperature ranged between 12°C and 25°C during the study period. Daily routines were similar to previous observation periods as detailed by Leonardi et al. (2010) and Buchanan-Smith et al. (2013). The main feeds were in the morning and afternoon (in the indoor enclosures), with scatter feeds being distributed throughout the rest of the day (usually in the outdoor enclosure before/during the afternoon educational talk).

Design and Procedure

Data were collected during June-August 2015 by G. B. Inter-observer reliability (IOR) was assured by learning from the principal investigator (S. D.) whilst observing the monkeys, and detailed unambiguous descriptions being available. We used scan sampling methods (Martin & Bateson, 2007) to record the location (*Sapajus/Saimiri* indoor or outdoor), zone and height occupied for each individual, sampling both species in the mixed-species groups. Scans were collected for all group members within 20 min intervals for either East or West. We first recorded each individual in the indoor enclosure (*Sapajus* followed by *Saimiri*), choosing individuals from left to right, then individuals in the outdoor enclosure and finally collecting data on any individuals who had not been recorded. If an individual was not observed during a scan then that individual would be recorded as out-of-sight. Each enclosure was divided and coded into meaningful zones (see Figures 1 – 2 and Table 2) and heights occupied were categorized as ground level, < 2 m, 2 – 4 m and > 4 m, following Leonardi et al. (2010). Recording took place between 09:00 and 17:00 hr, with a similar number of scans divided into three time frames: morning

Table 1

Study Subjects: East Sapajus (n =17), East Saimiri (n =17), West Sapajus (n =18), West Saimiri (n =9)

Name	Genus	Sex	Age range (in years) during study	Exhibit	# of observations (In/Out)
Popeye	<i>Sapajus</i>	M	13 – 14	East	11/79
Anita	<i>Sapajus</i>	F	17	East	17/70
Junon	<i>Sapajus</i>	F	14 – 15	East	7/83
Kato	<i>Sapajus</i>	M	9 – 10	East	20/70
Manuel	<i>Sapajus</i>	M	11	East	16/72
Penelope	<i>Sapajus</i>	F	9	East	14/72
Carlos	<i>Sapajus</i>	M	8 – 9	East	28/59
Chico	<i>Sapajus</i>	M	6	East	38/47
Rosa	<i>Sapajus</i>	F	5	East	18/67
Ruben	<i>Sapajus</i>	M	4 – 5	East	21/63
Sol	<i>Sapajus</i>	F	4 – 5	East	20/62
Flojo	<i>Sapajus</i>	M	3 – 4	East	16/72
Lindo	<i>Sapajus</i>	F	3 – 4	East	13/63
Willow	<i>Sapajus</i>	F	2	East	12/74
Nena	<i>Sapajus</i>	F	2	East	13/71
Gustavo	<i>Sapajus</i>	M	1	East	12/76
Agnes	<i>Sapajus</i>	F	1	East	11/77
Boa	<i>Saimiri</i>	M	9	East	23/37
Tatu	<i>Saimiri</i>	F	14	East	47/24
Roca	<i>Saimiri</i>	F	12	East	38/16
Maya	<i>Saimiri</i>	F	11	East	71/5
Elie	<i>Saimiri</i>	F	9	East	57/16
Cali	<i>Saimiri</i>	F	9	East	48/18
Pica	<i>Saimiri</i>	F	7	East	82/1
Yendi	<i>Saimiri</i>	F	6	East	29/34
Flora	<i>Saimiri</i>	F	6	East	40/19
Sipi	<i>Saimiri</i>	F	5	East	33/24
Lexi	<i>Saimiri</i>	F	4	East	32/28
Dora	<i>Saimiri</i>	F	4	East	45/17
Amarilla	<i>Saimiri</i>	F	3	East	37/32
Pelusa	<i>Saimiri</i>	F	3	East	32/29
Gabriela	<i>Saimiri</i>	F	3	East	53/9
Valencia	<i>Saimiri</i>	F	3	East	42/25
Ciara	<i>Saimiri</i>	F	3	East	40/26
Diego	<i>Sapajus</i>	M	12 – 13	West	52/38
Lana	<i>Sapajus</i>	F	19	West	43/44
Santiago	<i>Sapajus</i>	F	13	West	45/44
Sylvania	<i>Sapajus</i>	F	11 – 12	West	38/47
Toka	<i>Sapajus</i>	M	10	West	46/43
Figo	<i>Sapajus</i>	M	9	West	33/52
Pedra	<i>Sapajus</i>	F	7	West	47/42
Mekoe	<i>Sapajus</i>	M	7	West	58/27
Inti	<i>Sapajus</i>	M	5	West	28/54
Rufo	<i>Sapajus</i>	M	5	West	29/56
Ximo	<i>Sapajus</i>	M	5	West	42/44
Torres	<i>Sapajus</i>	M	4	West	38/43
Luna	<i>Sapajus</i>	F	4	West	48/37
Alba	<i>Sapajus</i>	F	3	West	51/39
Mr Fudge	<i>Sapajus</i>	M	1 – 2	West	47/43
Bear	<i>Sapajus</i>	M	1 – 2	West	50/39
Hazel	<i>Sapajus</i>	F	1	West	47/39
Pixie	<i>Sapajus</i>	F	1	West	45/41
Hugo	<i>Saimiri</i>	M	4 – 5	West	47/20
Gerda	<i>Saimiri</i>	F	15	West	87/0
Jasmin	<i>Saimiri</i>	F	12	West	83/3
Toomi	<i>Saimiri</i>	F	8	West	73/14
Dita	<i>Saimiri</i>	F	5	West	75/9
Sancha	<i>Saimiri</i>	F	5	West	80/5
Orla	<i>Saimiri</i>	F	3	West	77/4

Table 1 (cont.)

Gisele	<i>Saimiri</i>	F	2 – 3	West	79/4
Loki	<i>Saimiri</i>	F	1	West	64/22

(09:00 – 12:00), midday (12:00 – 14:00) and afternoon (14:00 – 17:00). We accumulated a total of 180 scans divided equally between East and West.

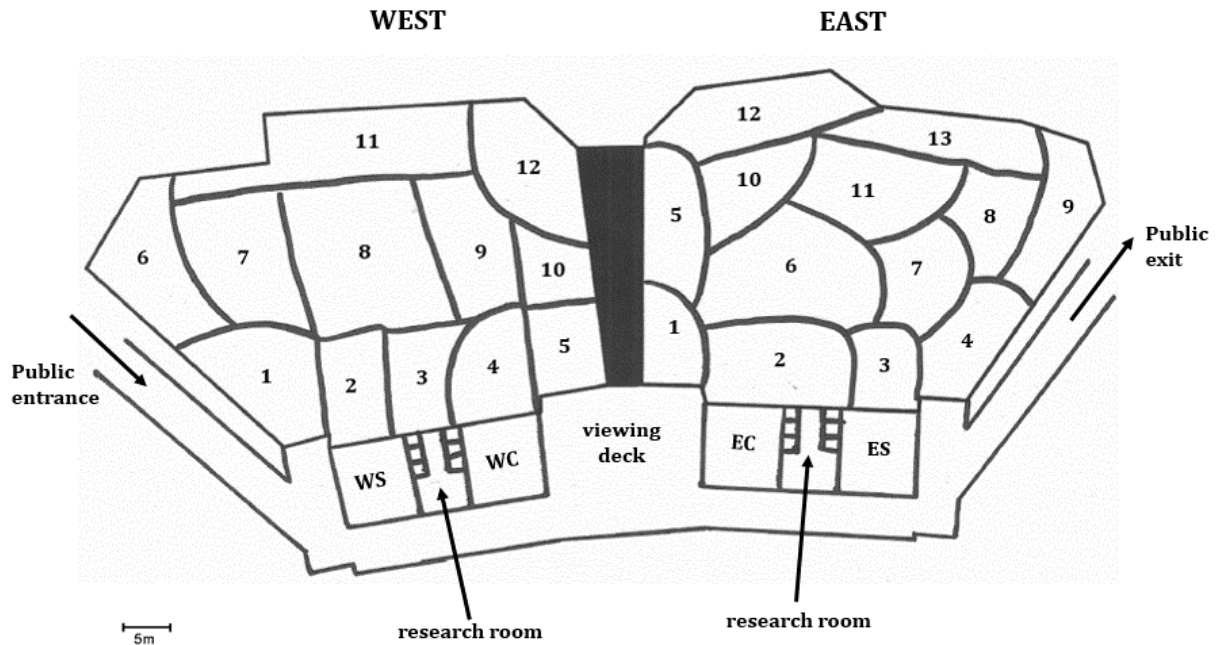


Figure 1. Schematic diagram of the Living Links to Human Evolution Research Centre outdoor enclosures, divided into “meaningful zones” (approximately to scale), for example zone 2 East represents woodchip and tree logs on the ground and zone 3 West represents tall grass and wild flowers (see Table 2 for more details of zones). Key for indoor enclosures: WS and WC = West squirrel monkeys and West capuchins; ES and EC = East squirrel monkeys and East capuchins.

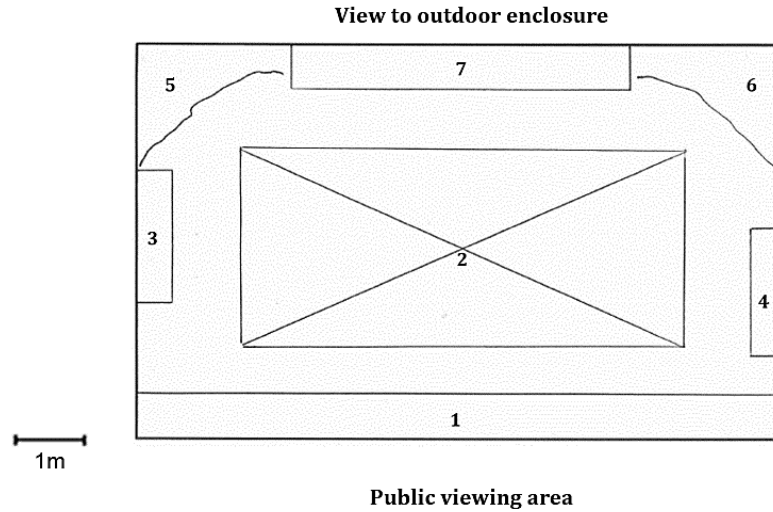


Figure 2. Schematic diagram of the Living Links to Human Evolution Research Centre, *Sapajus* indoor enclosure, divided into meaningful zones (approximately to scale): (1) large window and window sill where the visitors can see into the indoor enclosure; (2) the central tree log platforms and scaffolding, in a rectangular shape with criss-crossing sections (on two levels), and surrounding blank areas; (3) small upper window and window sill (on the right of the West *Saimiri* and East *Sapajus* and on the left of the West *Sapajus* and East *Saimiri*); (4) large lower window and window sill – can see into the cubicle research area (on the left of the West *Saimiri* and East *Sapajus* and on the right of the West *Sapajus* and East *Saimiri*); (5) Rock wall and rock ledge to the back left of the enclosure; (6) rock wall and rock ledge to the back right of the enclosure; (7) large window and window sill at the back of the enclosure.

Table 2

Descriptions of the “Meaningful Zones” within the West and East Outdoor Enclosures

Zone	West	East
1	Large rocks protruding from the ground	Large rocks protruding from the ground and long tree logs
2	Large rocks protruding from the ground and long tree logs	Woodchip on ground and tree logs
3	Tall grass and wild flowers	Woodchip on ground and vines leading to small tree
4	Woodchip on ground, tree log and grass	Shrubbery and evergreen bushes
5	Large rocks protruding from the ground and long tree logs	Evergreen bushes running parallel to the fence line
6	Evergreen bushes	Small tree (looks like a Y shape), cluster of tall trees and short grass
7	Tree stump and tall trees in the shape of an H with a slanted/diagonal middle section (tree log) and bamboo	Group of 4 trees
8	Cluster of central tall trees, with resting platforms	Small pine trees and tall grass
9	Smaller trees and grass section	Evergreen bushes and tall grass
10	Large rocks protruding from the ground	Forked tree and flat platforms
11	Shrubbery, bushes and tall grass	Trees towards the back of the enclosure with wavy branches between trees
12	Tall grass and tree log	Tall grass and shrubbery
13	–	Tall grass

Data Analysis

In order to determine how selectively *Sapajus* and *Saimiri* used their enclosure space, we calculated a modified spread of participation index (SPI) (Plowman, 2003) using the following formula:

$$\text{SPI} = \frac{\sum |f_o - f_e|}{2(N - f_{e \min})}$$

where f_o is the frequency of observations in a zone or height level, f_e the expected frequency of observations in a zone or height level, based on zone size or height assuming even use of the whole enclosure, $|f_o - f_e|$ is the absolute value of the difference between f_o and f_e , which is summed for all zones or height levels Σ , N the total number of observations and $f_{e \min}$ the expected frequency of observations in the smallest zone or height.

The modified formula was used over the original formula by Dickens (1995), because it allows for unequal zones (Plowman, 2003). The index varies between 0 and 1, with 0 suggesting maximum enclosure use (i.e., all zones and heights occupied equally) and a value of 1 suggesting minimum use of enclosure (i.e., only one zone or height occupied).

Mann-Whitney tests were used to determine whether the observed data for zones and heights occupied were consistent with the values expected under the fitted model (Field, 2009). Linear regressions were used to determine whether age can explain variation in enclosure use based on SPI values, and Wilcoxon's test was applied to SPI data for 3-D indoor and outdoor enclosure use.

The research was approved by the Psychology Ethics Committee at the University of Stirling, Scotland and abided by the Association for the Study of Animal Behavior Ethical Guidelines (ASAB, 2007).

Results

Enclosure Use

We calculated percentages of each species occupying each enclosure (indoor/outdoor). Had we found support for attraction (indirect indicator of potential for cognitive enrichment), we would have expected there to be a high percentage of both species occupying the same enclosures. The species were co-present for 84% in the East, and only 34% in the West (see Table 3).

Table 3
The Percentage of Scans ($n = 90$) Spent in Enclosures, Out of Sight, and Co-present for Both East and West Groups

Exhibit	Species	% indoor enclosure(s)	% outdoor enclosure	% out of sight	% co-present
East	<i>Sapajus</i>	16	80	4	84
	<i>Saimiri</i>	57	27	16	
West	<i>Sapajus</i>	47	49	4	34
	<i>Saimiri</i>	88	11	1	

Both *Sapajus* groups showed a preference for the central tall tree areas of their outdoor enclosures, with the East group observed in zone 6 for 48% of scans (Figure 3A) and the West group in zone 8 for 36% of scans (Figure 3C). Although both *Sapajus* groups appear to make use of most of their outdoor enclosure space, peripheral zones were utilized less than expected. For the East group, zone 1 which included substrates such as large rocks and long tree logs was significantly underutilized ($U = 57$, $z = -3.029$, $p = 0.002$, $r = -0.73$), as well as woodchip areas, zone 2 ($U = 86$, $z = -2.017$, $p = 0.044$, $r = -0.49$) and zone 3 ($U = 38$, $z = -3.677$, $p < 0.0001$, $r = -0.89$) in addition to areas with shrubbery and

evergreen bushes, zone 5 ($U = 41.5$, $z = -3.605$, $p < 0.0001$, $r = -0.87$). Similarly, for West *Sapajus* areas including large rocks and long tree logs, zone 1 ($U = 60$, $z = -3.277$, $p = 0.001$, $r = -0.77$), zone 2 ($U = 17$, $z = -4.607$, $p < 0.0001$, $r = -1.09$) and zone 5 ($U = 64.5$, $z = -3.121$, $p = 0.002$, $r = -0.74$) and areas with shrubbery, evergreen bushes and tall grass, zone 6 ($U = 36$, $z = -4.205$, $p < 0.0001$, $r = -0.99$) were significantly underutilized.

By contrast both *Saimiri* groups showed a preference for peripheral areas of their outdoor enclosure with a high percentage of scans being in proximity to the indoor enclosure entrances. The East group were observed in zones 2 and 3 for 24% and 34% of scans respectively (Figure 3B) and the West group in zone 2 for 60% of scans (Figure 3D). For both *Saimiri* groups the central tree areas were utilized significantly less than expected; East, zone 6 ($U = 28$, $z = -4.022$, $p < 0.001$, $r = -0.98$) and zone 7 ($U = 46$, $z = -3.427$, $p = 0.001$, $r = -0.83$); West, zone 7 ($U = 13.5$, $z = -2.498$, $p = 0.013$, $r = -0.83$), zone 8 ($U = 10.5$, $z = -2.705$, $p = 0.01$, $r = -0.90$) and zone 9 ($U = 11.5$, $z = -2.683$, $p = 0.01$, $r = -0.89$). Other areas that were significantly underutilized by East *Saimiri* were zones including trees, zone 8 ($U = 17$, $z = -4.64$, $p < 0.001$, $r = -1.13$), zone 10 ($U = 15.5$, $z = -4.695$, $p < 0.0001$, $r = -1.14$) and zone 11 ($U = 17$, $z = -4.64$, $p < 0.001$, $r = -1.13$) and tall grass, zone 13 ($U = 17$, $z = -4.64$, $p < 0.001$, $r = -1.13$). The West *Saimiri* were also observed significantly less than expected in zones that were towards the back of the outdoor enclosure, zone 6 ($U = 4.5$, $z = -3.514$, $p < 0.001$, $r = -1.17$), zone 9 ($U = 11.5$, $z = -2.683$, $p = 0.01$, $r = -0.89$) and zones 10, 11 and 12 ($U = 4.5$, $z = -3.492$, $p < 0.001$, $r = -1.16$).

For indoor enclosure use, both the East and West *Sapajus* groups and West *Saimiri* group were observed for a high proportion of scans in zone 2 (the central rectangular, with crisscrossing mid sections, log platforms and scaffolding), 70%, 68%, and 72% respectively (Figure 4A, C, D). While the East *Saimiri* were observed using zone 7 (the large window and window sill at the back of the enclosure) for 40% of scans (Figure 4B). In the East *Sapajus* enclosure zone 5, the rock wall and rock ledge to the back left of the enclosure ($U = 84$, $z = -2.121$, $p = 0.034$, $r = -0.51$) and zone 7 ($U = 18$, $z = -4.461$, $p < 0.001$, $r = -1.08$) were utilized significantly less than expected. Both East *Saimiri* ($U = 55$, $z = -3.097$, $p = 0.002$, $r = -0.75$) and West *Sapajus* ($U = 57$, $z = -3.335$, $p = 0.001$, $r = -0.79$) were observed in zone 1 (the large window and window sill where visitors can see into the indoor enclosure) significantly less than expected. Whereas the West *Saimiri* significantly underutilized zone 3 ($U = 11$, $z = -2.655$, $p = 0.01$, $r = -0.89$), zone 4 ($U = 9$, $z = -2.929$, $p = 0.003$, $r = -0.98$), zone 6 ($U = 13$, $z = -2.433$, $p = 0.015$, $r = -0.81$) and zone 7 ($U = 0.0$, $z = -3.593$, $p < 0.001$, $r = -1.20$). Observations of monkeys in zone 4 (large lower window and window sill – can see into the cubicle research area) were rare or did not occur during sampling.

Heights Occupied

The data presented in Figures 5 and 6 show the observed and expected values of heights occupied by the East and West groups of *Sapajus* and *Saimiri* in their indoor and outdoor enclosures. The percentage of *Sapajus* and *Saimiri* at each height level is relatively similar between the East and West groups, and they appear to be well distributed across the vertical space, though they were all observed significantly less than expected at ground level when indoors (Figure 5); East *Sapajus* ($U = 85$, $z = -2.1$, $p = 0.036$, $r = -0.51$) East *Saimiri* (ground, $U = 34$, $z = -3.982$, $p < 0.001$, $r = -0.97$; <2m, $U = 84$, $z = -0.86$, $p = 0.04$, $r = -0.51$), West *Sapajus* ($U = 18$, $z = -4.828$, $p < 0.001$, $r = -1.14$), West *Saimiri* ($U = 18$, $z = -2.049$, $p = 0.04$, $r = -0.68$). Both groups of *Saimiri* were observed occupying heights of 2-4m (East, $U = 64$, $z = -2.79$, $p = 0.005$, $r = -0.68$; West, $U = 15.5$, $z = -2.311$, $p = 0.021$, $r = -0.77$) and > 4m (East, $U = 22.5$, $z = -4.361$, $p < 0.001$, $r = -1.06$; West, $U = 4.5$, $z = -3.492$, $p < 0.001$, $r = 1.16$) significantly less than expected (Figure 6B, C). No significant differences were found between observed and expected values for the vertical distribution of East or West *Sapajus* (Figure 6A, C) in their outdoor enclosures ($p > 0.05$).

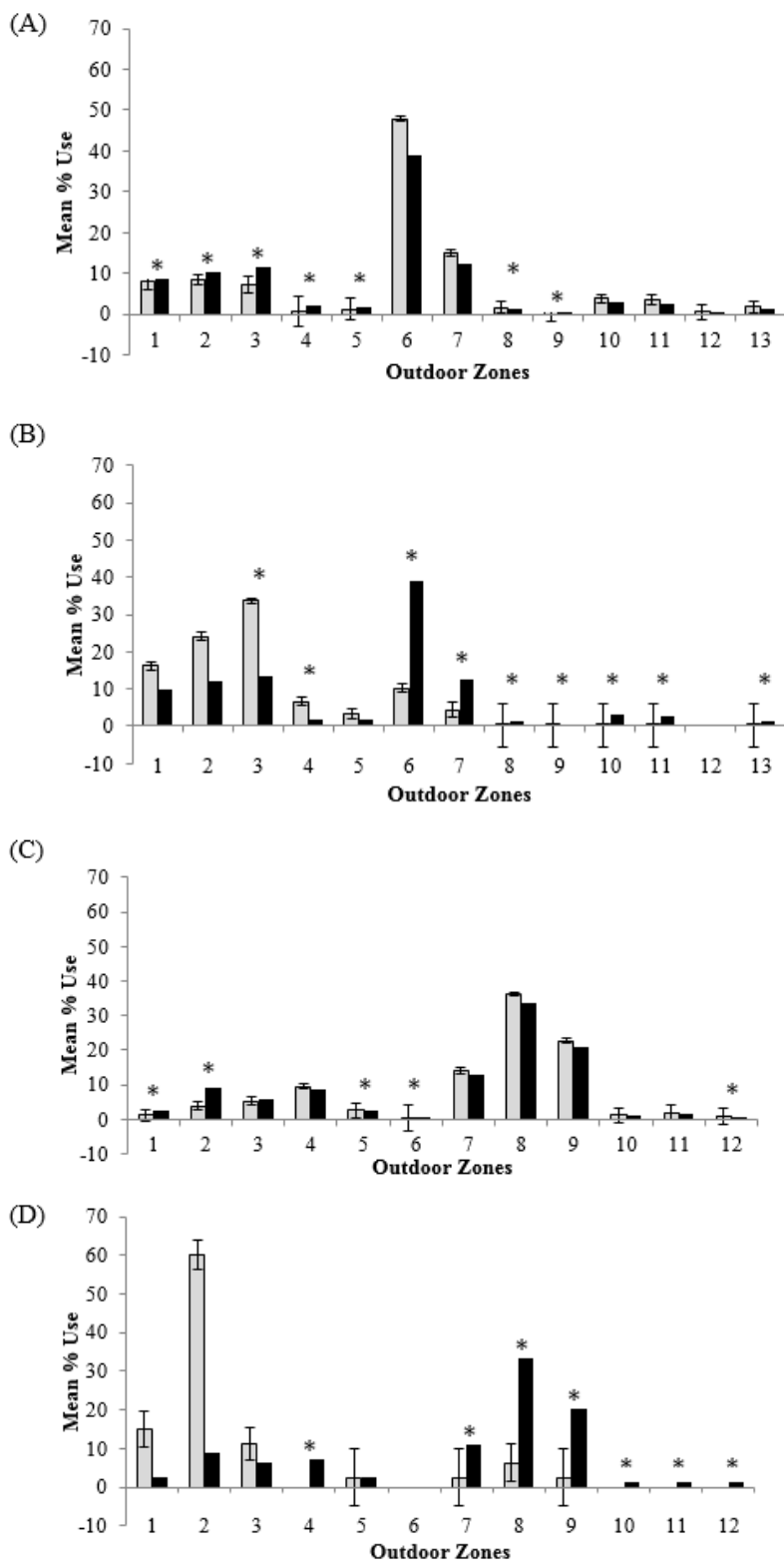


Figure 3. Zone use in East and West outdoor enclosures ($n = 90$) including \pm S.E bars for (A) East *Sapajus*, (B) East *Saimiri*, (C) West *Sapajus*, and (D) West *Saimiri*. An asterisk (*) indicates a significant difference between observed (light bars) and expected (dark bars) values.

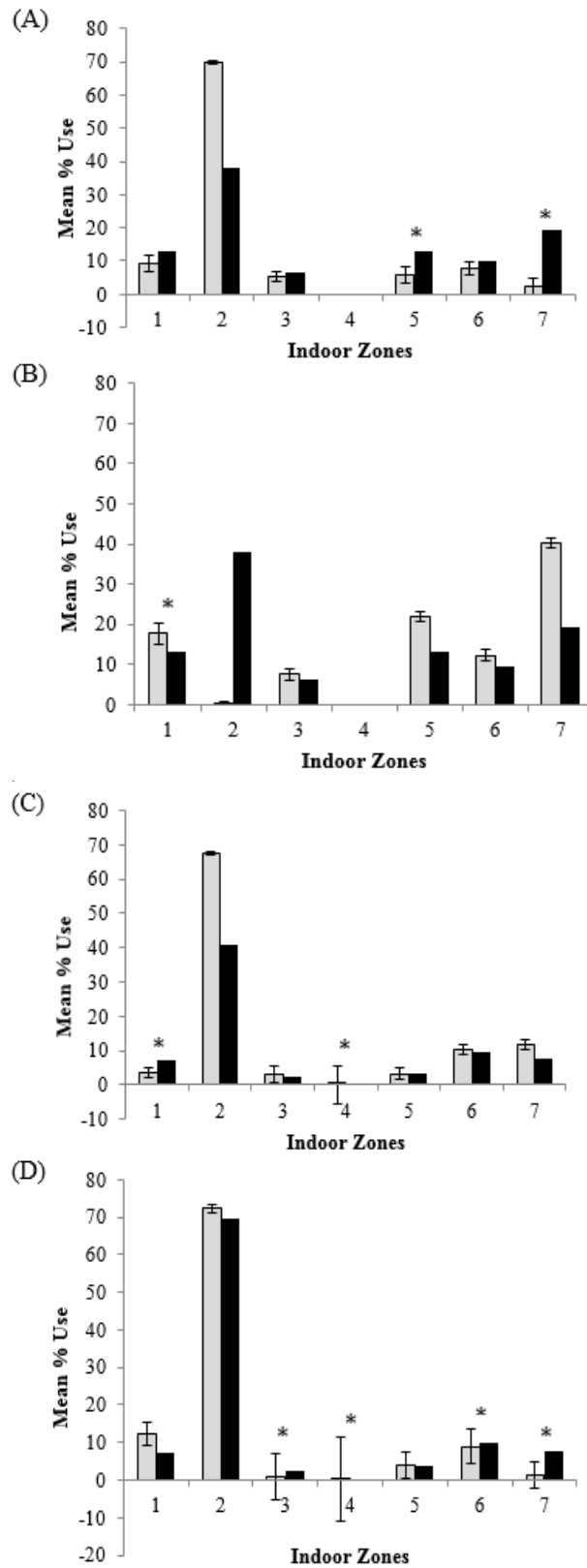


Figure 4. Zone use in East and West indoor enclosures ($n = 90$) for (A) East *Sapajus*, (B) East *Saimiri*, (C) West *Sapajus*, and (D) West *Saimiri*. An asterisk (*) indicates a significant difference between observed (light bars) and expected (dark bars) values.

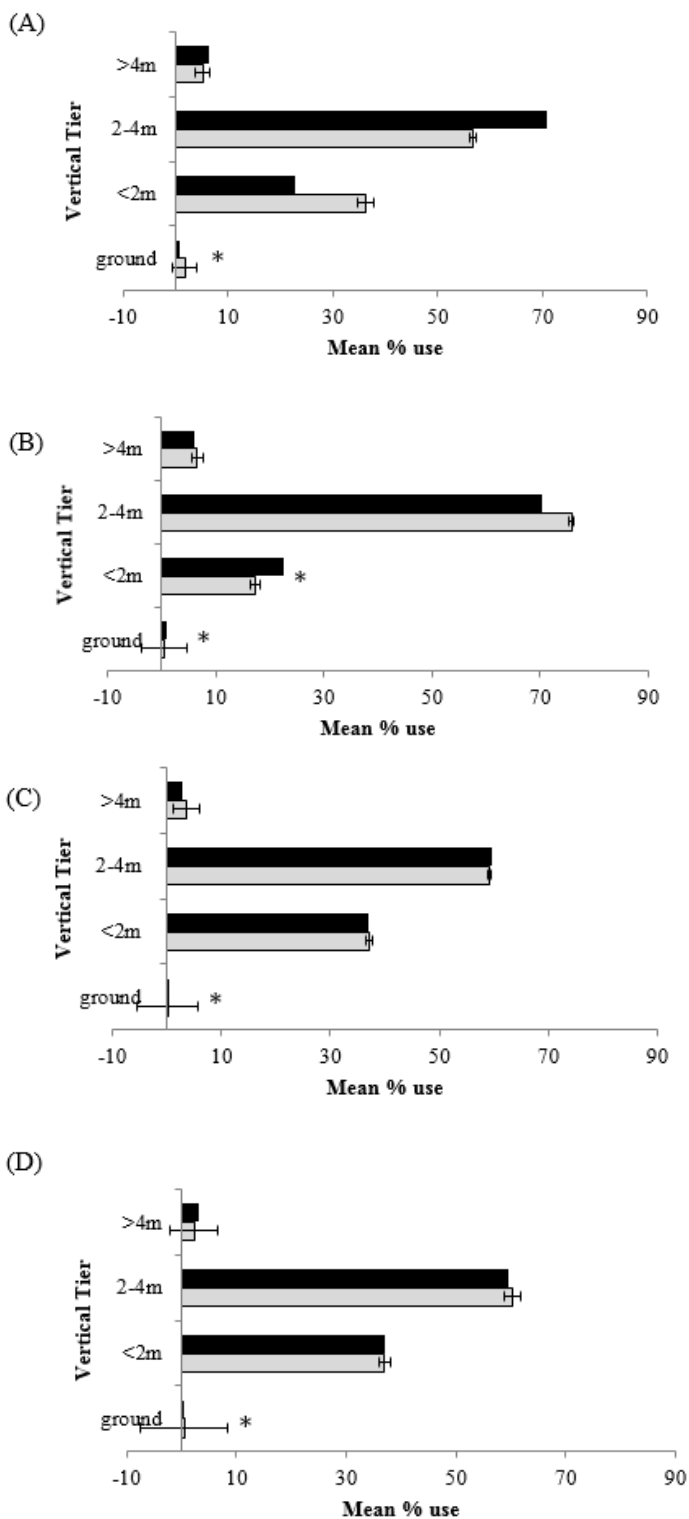


Figure 5. Use of four vertical tiers in the East and West indoor enclosures ($n = 90$) including \pm SE bars for (A) East *Sapajus*, (B) East *Saimiri*, (C) West *Sapajus*, and (D) West *Saimiri*. An asterisk (*) indicates a significant difference between observed (light bars) and expected (dark bars) values.

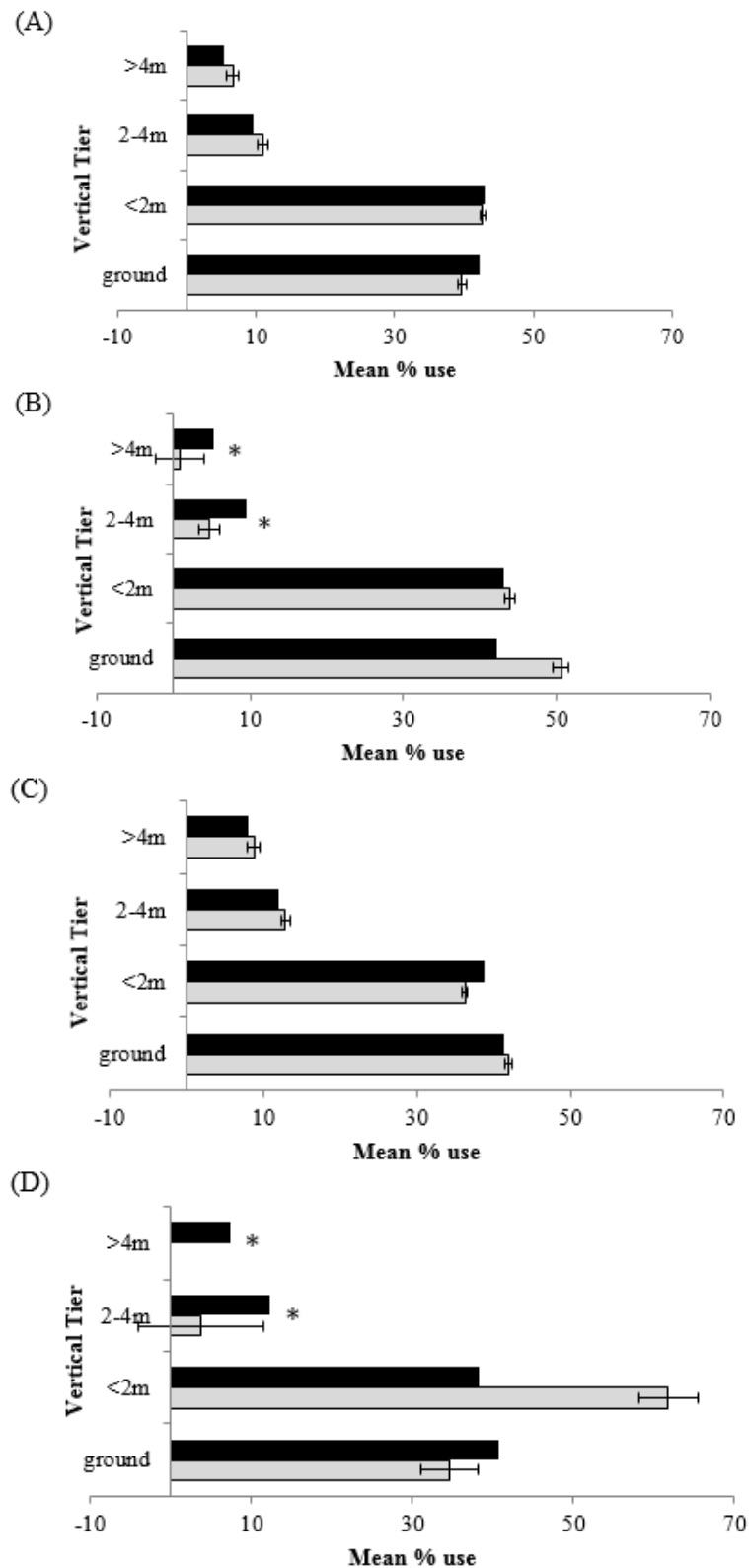


Figure 6. Use of four vertical tiers in the East and West outdoor enclosures ($n = 90$) including \pm SE bars for (A) East *Sapajus*, (B) East *Saimiri*, (C) West *Sapajus*, and (D) West *Saimiri*. An asterisk (*) indicates a significant difference between observed (light bars) and expected (dark bars) values.

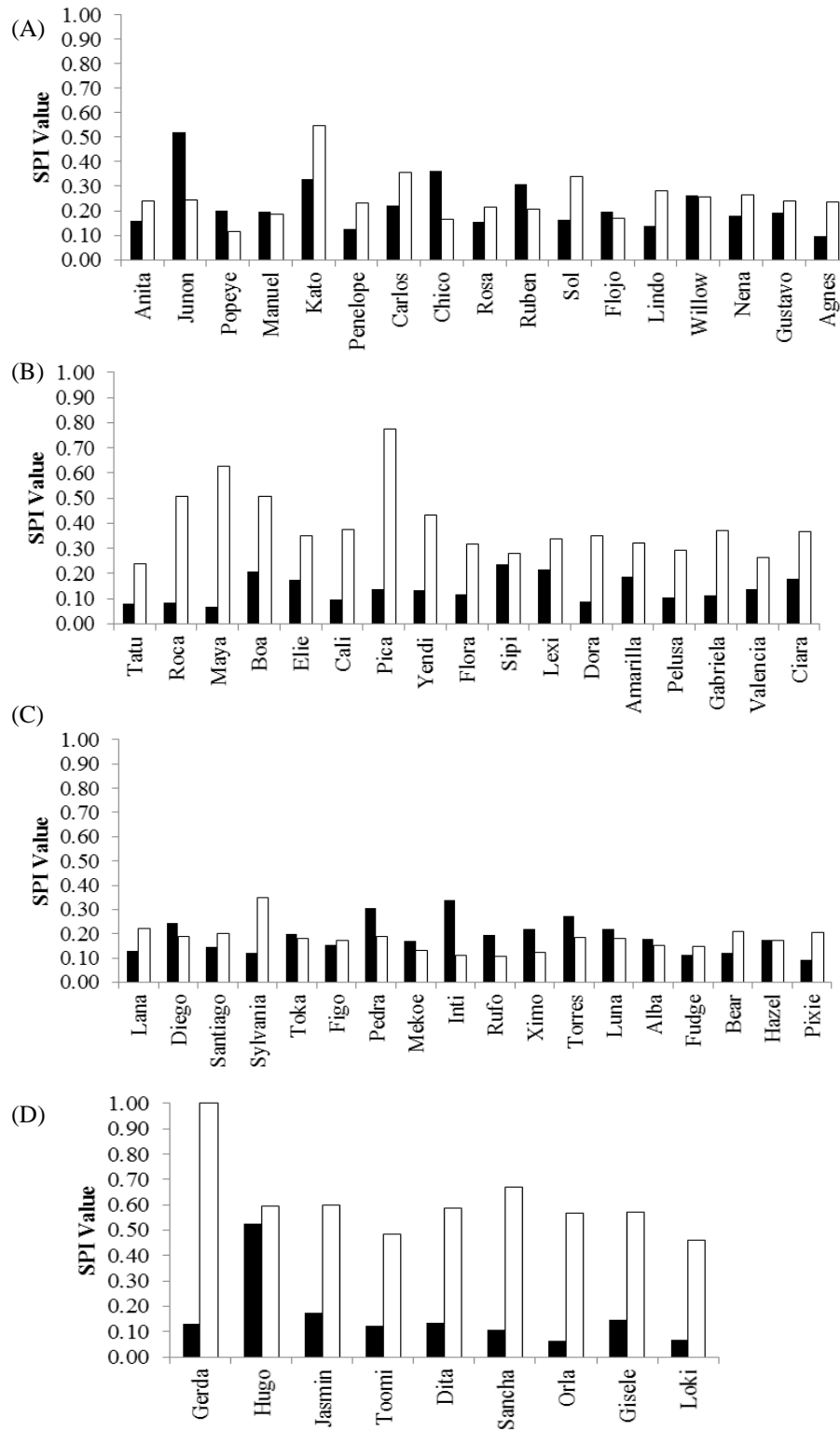


Figure 7. The Spread of Participation Index for indoor (dark bars) and outdoor (light bars) 3D enclosure in East and West groups; (A) East *Sapajus*, (B) East *Saimiri*, (C) West *Sapajus*, and (D) West *Saimiri*. Individuals are listed by age (oldest from left to youngest right). SPI values that are closer to 0 suggest maximum enclosure use (i.e., all zones and heights occupied equally) and a value of 1, minimum use of enclosure (i.e., only one zone or height occupied).

Spread of Participation Index

Combined Spread of Participation Index (SPI) values were calculated for zone use and heights occupied in order to determine 3D space use for all individuals, and the results indicate that overall *Saimiri* utilized less of the 3D space in their outdoor enclosures (East $M_{SPI} = 0.33$, West $M_{SPI} = 0.85$) than *Sapajus* (East $M_{SPI} = 0.10$, West $M_{SPI} = 0.06$), and the East groups utilized the 3D space in their indoor enclosures less (*Sapajus* $M_{SPI} = 0.25$; *Saimiri* $M_{SPI} = 0.23$) compared to the West groups (*Sapajus* $M_{SPI} = 0.10$; *Saimiri* $M_{SPI} = 0.04$). However, when considering individual differences within groups we can see that certain individuals better utilize the available space than others (Figure 7). If younger individuals required more space than adults then we may expect to see lower SPI values for subadults. Linear regression analyses were performed to test whether there would be a relationship between age and enclosure use, based on combined SPI scores.

In the East groups, the results indicated that age could not predict indoor enclosure use for *Sapajus* ($b = 0.714$), explaining 11.3% of the variance, which was not significant, $R^2 = 0.113$, $F(1, 16) = 1.914$, $p = 0.187$. The results also were non-significant for outdoor enclosure use ($b = 0.002$), where age explained 0% of the variance, $R^2 = 0.002$, $F(1, 16) = 0.00$, $p = 0.997$. For the East *Saimiri*, age ($b = -0.608$) explained 16.8% of the variance in indoor enclosure, which was not significant, $R^2 = 0.168$, $F(1, 16) = 3.023$, $p = 0.103$. Neither were the results for outdoor enclosure use ($b = 1.235$), which explained 17.1% of the variance, $R^2 = 0.171$, $F(1, 17) = 3.305$, $p = 0.088$.

The results for West *Sapajus* indicate that age could not predict indoor ($b = -0.069$) or outdoor ($b = 0.459$) enclosure use. Age explained 0.2% of the variance for indoor enclosure use, $R^2 = 0.002$, $F(1, 17) = 0.00$, $p = 0.846$, and 17.1% of the variance for outdoor enclosure use, $R^2 = 0.171$, $F(1, 17) = 3.305$, $p = 0.088$, both of which were non-significant. Similarly for West *Saimiri* indoor ($b = 0.141$) enclosure use, age was found to explain 0.2% of the variance for indoor enclosure use, which was not significant, $R^2 = 0.002$, $F(1, 8) = 0.014$, $p = 0.908$. However age significantly predicted outdoor enclosure use ($b = 2.498$) explaining 52% of the variance, $R^2 = 0.520$, $F(1, 8) = 7.597$, $p = 0.028$.

Furthermore, Wilcoxon's test confirmed significant differences between indoor and outdoor enclosure use in *Saimiri*, indicating avoidance behavior. For East *Saimiri*, SPI values for enclosure use were significantly lower indoors ($Mdn = 0.13$) than outdoors ($Mdn = 0.35$), $z = -3.623$, $p < 0.001$, $r = -0.88$. Similarly for West *Saimiri* SPI values for enclosure use were significantly lower indoors ($Mdn = 0.13$) than outdoors ($Mdn = 0.59$), $z = -2.668$, $p < 0.008$, $r = -0.89$.

Discussion

Although efforts are increasingly made to provide for the physical and psychological needs of animals in captivity, social enrichment is often neglected. Non-human primates are known to have larger brains (in relation to body size) than other mammals of equivalent size (Barrett & Henzi, 2005; Shultz & Dunbar, 2007). This has been causally linked as a selective pressure for primate intelligence (Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966), for instance being socially vigilant (i.e., learning to avoid problematic or stressful situations) may provide a prime reason for exercising a large brain. Our data supplement previous research (Buchanan-Smith et al., 2013; Leonardi et al., 2010) on the two mixed-species communities at the Living Links to Human Evolution Research Centre, RZSS Edinburgh Zoo highlighting the ever-changing dynamics, challenges and complexity of group living in captivity.

Based on previous research of mixed-species associations in captivity (Buchanan-Smith, 2013; Leonardi et al., 2010) and the wild (Fleagle et al., 1981; Podolsky, 1990; Terborgh, 1983), we wanted to assess whether the two species were attracted to each other (an indirect indicator of the potential for cognitive enrichment), and predicted that if this was the case then we would expect them to occupy the same spaces in their shared enclosures. However, our data did not support this prediction. Whilst East *Sapajus* and *Saimiri* were present in the same enclosures for 84% of scans ($n = 90$), which is in keeping with previous findings (see Buchanan-Smith et al., 2013), the results for West *Sapajus* and *Saimiri* showed a substantial decrease in the percentage of scans spent in shared enclosures (34%, $n = 90$).

compared to previous data. This decrease may be attributed to the change in the composition and number of individuals in the West *Saimiri* group from 15 individuals (2008 – 09), 10 individuals (2010) and 9 individuals (2015), providing an imbalance with the number of *Sapajus* ($n = 18$). Group size varied as individuals were removed for husbandry purposes, to prevent intraspecific aggression and because a new and younger alpha male was introduced (see Buchanan-Smith et al., 2013). East and West *Sapajus* groups were observed more than would be expected in the central zones (where tall trees were present) of their outdoor enclosures and appeared to use all available space. While East and West *Saimiri* groups were observed more than would be expected in peripheral zones of their outdoor enclosure with a high percentage of scans being in proximity to indoor enclosure entrances. This along with the significant difference between indoor and outdoor enclosure use for *Saimiri* further suggests that they are avoiding interactions with *Sapajus* and are possibly staying closer to indoor enclosure entrances as an escape option.

Although avoidance behavior may be considered as being detrimental to the welfare of *Saimiri*, in the wild it is natural to be vigilant of the whereabouts of more dominant species and predators, and promotion of natural behavior is a goal of environmental enrichment as long as it is not detrimental to animal health (Buchanan-Smith, 2010; Chamove & Anderson, 1989; Moodie & Chamove, 1990). It may even be construed as providing appropriate cognitive challenges for the less dominant *Saimiri* (Buchanan-Smith et al., 2013; Clark, 2011). The habitual use and clustering of highly used areas has been reported in other studies of captive primates (Mallapur et al., 2005; Ogden et al., 1990; Ross et al., 2009; Stoinski et al., 2000), and could indicate that habitat use may also be dependent on functionality (i.e., locations with the greatest utility). For instance, the zones in the outdoor enclosure occupied by *Saimiri* included substrates such as connecting evergreen bushes, which provides adequate cover from potential aerial predators and opportunities for “natural” foraging (insects). Furthermore, the majority of the outdoor enclosure encompasses large open spaces with travel between zones made possible only by moving at ground level. It was found that *Saimiri* tended to occupy the mid to lower levels (0 – 2m and 2 – 4 m) in both indoor and outdoor enclosures, which is consistent with wild data (Boinski, 1999; Fleagle et al., 1981), though the East *Saimiri* were also observed for an unexpectedly high proportion of time at ground level. *Sapajus* on the other hand were distributed across all levels, in both indoor and outdoor enclosures which is relatively consistent with wild data, whereby *Sapajus* occupy the middle to lower levels of the main canopy (Fleagle et al., 1981), reinforcing the importance of providing sufficient climbing opportunities for both species.

The age of individuals in relation to space use was also considered. Subadults, though smaller than adults, are usually found to be more active than adults, and may have greater space requirements for physical development and play (Traylor-Holzer & Fritz, 1985; Wells & Turnquist, 2001). Therefore, we predicted that subadults would utilize more space than adults. However, our data did not support this prediction as no significant relationship was found between age and enclosure use other than for the West *Saimiri*, which may have been due to the small sample size (9 individuals) compared with the other groups (see Table 1).

Providing appropriate and enriching environments that are both physically and socially complex in captivity can be very challenging, especially in terms of mimicking natural group size and structure. However, it is critical to find ways in which to include complexity so as to minimize negative welfare states such as boredom, apathy and fear, and to promote positive welfare states of security, with opportunities for achievement (Poole, 1991).

Housing naturally associating species such as *Sapajus* and *Saimiri* (Klein & Klein, 1973; Fleagle et al., 1981; Podolsky, 1990; Terborgh, 1983) in mixed exhibits is one way to provide more complexity within the captive environment and to promote the increase of positive (and more “natural”) species-specific behaviors (Dalton & Buchanan-Smith, 2005; Stoinski et al., 2000). The Living Links to Human Evolution Research Centre was built specifically for *Sapajus* and *Saimiri*, and the design took into account a considerable number of factors that included ecological differentiation, different locomotor patterns and preferred support orientations and size (Buchanan-Smith et al., 2013; Poole, 1991). When efforts such as these are made, utilizing our knowledge of the social environments that are species typical

in the wild in order to create a captive environment that allows animals to develop and display natural behaviors can have a positive effect on their welfare (Visalberghi & Anderson, 1993). However, as *Sapajus* are approximately three times the size of *Saimiri*, and are the more dominant species in their associations in their natural habitat (Podolsky, 1990; Terborgh, 1983), there may be potential welfare concerns. As such, and given the difficulties in predicting the ever-changing social dynamics of groups, providing separate enclosures for *Saimiri*, which *Sapajus* are unable to enter, was crucial in giving them the choice to avoid *Sapajus*, and provide them with an area where they could feel secure (Buchanan-Smith et al., 2004; Buchanan-Smith et al., 2013; Fritz & Nash, 1983; Maple, 1979; Maple & Stine, 1982). This enables an appropriate cognitively challenging environment (Carlstead & Shepherdson, 2000) whereby *Saimiri* are able to actively control and explore their environment.

The utilization of specific areas of both indoor and outdoor enclosures observed in this study suggest some important points for the monitoring of animals housed in mixed-species exhibits. Our findings indicate that mixed-species living is more cognitively challenging than cognitively enriching, but with careful monitoring and formal data collection we can ensure that intentionally bringing the two species into a shared exhibit is not detrimental to their welfare.

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